Description of a new genus and species of Pseudothelphusidae Ortmann, 1893 (Decapoda: Brachyura) from Panama, and new records and remarks on the zoogeography of Trichodactylus quinquedentatus Rathbun, 1893 (Trichodactylidae) in Central America

Célio Magalhães¹, and Peter K.L. Ng²

¹Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, 69067–375 Manaus, Amazonas, Brazil; and ²Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore

Correspondence: Célio Magalhães; email: celiomag@inpa.gov.br

(Received 30 August 2018; accepted 24 October 2018)

ABSTRACT

A collection of freshwater crabs from Central America resulted in the description of a new genus and two new species of pseudothelphusid crabs from Panama, and the record of the trichodactylid Trichodactylus quinquedentatus Rathbun, 1893 from Honduras and Panama. A new monotypic genus, Emberacarcinus n. gen., is erected to accommodate Potamocarcinus darienensis Magalhães, Campos & Türkay, 2013. The two new species and can be distinguished from their respective congeners by the structures of the male first gonopods: Ptychophallus bilobatus n. sp. has a bilobed mesial process whereas Potamocarcinus tapirrhynchus n. sp. exhibits a mesial process as a stout, rounded projection obliquely directed apical-cephalically and partially fused to the mesial lobe of the apical crest. The taxonomic affinities of both species with their closest congeners are treated, and the zoogeographic implication of the new records of T. quinquedentatus in Central America is discussed.

Key Words: biodiversity, biogeography, Central and South American freshwater fauna, Neotropical region, taxonomy

INTRODUCTION

Panama harbors a remarkably rich freshwater crab fauna despite its relatively small territory (75,517 km²). Our knowledge of this fauna began in the late nineteenth century with the description of Pseudothelphusa colombianus Rathbun, 1893 (now in Ptychophallus Smalley, 1964) from the Chiriquí province, but increased mainly during the second half of the twentieth century with the descriptions of several new taxa by Pretzmann (1965, 1968a, 1968b, 1971, 1978), Rodríguez (1994), Campos & Lemaitre (1999, 2002), and Magalhães et al. (2013). Ábrego & Cornejo (2015) provided a checklist of freshwater decapods from Panama based on the records available in the literature, and listed 20 species of freshwater crabs. Although their list included incertae sedis taxa and some species with unconfirmed records, this number is close to the 17 species currently recognized in the country (Magalhães et al., 2015). Such diversity of the Panamanian freshwater crab fauna is similar to that of Costa Rica (15 species) and Guatemala (17 species), the other Central American countries recently surveyed for this group (Magalhães et al., 2015; Wehrtmann et al., 2016).

The Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum (previously Raffles Museum), National University of Singapore has accumulated a small but important collection of freshwater brachyuran crabs. Some of this material has already been used in other studies (e.g., Ng & Guinot, 2001; Shih et al., 2015; Ng & Castro, 2016). ZRC passed the collection of Neotropical crabs to the first author for study as part of his revision of the Neotropical fauna. The taxonomic and zoogeographic results derived mainly from the study of this material are reported here.

MATERIALS AND METHODS

Specimens are deposited at the Colección Zoológica Dr. Eastorgio Méndez, Instituto Conmemorativo de Estudios de la Salud (CoZEM), Panama City, Panama; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Museu de Zoologia, Universidade de São Paulo (MZUSP), São Paulo, Brazil; National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C.; and ZRC. Measurements of carapace are in...
millimeters, carapace width was measured across the carapace at its widest point, and carapace length was measured along the midline, from the frontal to the posterior carapace margin. Both measurements follow the number and sex of the specimens examined and are given between parenthesis as (carapace breadth × carapace length). The following abbreviations are used in the text: carapace width (cw), carapace length (cl), male first (G1) and second (G2) gonopods, third maxillipeds (max3), cheliped (P1), pereiopods 2 to 5 (P2–P5), and sternal sulci between adjacent thoracic sternites (s4/s5). Localities without geographic coordinates were georeferenced using Google Earth® software and GeoNames (http://www.geonames.org/), and the coordinates given in brackets. The distribution maps were generated using the QGIS software, v. 2.14.16 (http://www.qgis.org/ptBR/site/). Line drawings were made by CM with the aid of a Wild M8 (Wild, Heerbrugg, Switzerland) stereomicroscope equipped with a drawing tube, then scanned and edited in Adobe Photoshop® CS 2 software. The plates were mounted in CorelDraw® X3 software. Terminology used in the description of the G1 was adapted from Smalley (1964a), Villalobos & Álvarez (2010), and Magalhães et al. (2015).

SYSTEMATICS

Family Pseudothelphusidae Ortmann, 1893

Tribe Hypolobocerini Pretzmann, 1971

Genus Ptychophallus Smalley, 1964

Ptychophallus colombianus (Rathbun, 1893)

(Figs. 1A–C, 8)

Material examined: 1 male (37.0 × 22.7), ZRC 2015.0023, Panama, Chiriquí province, Boquete, Bajo Mono [~08°48ʹ N 82°27ʹ W], ~1,730 m above sea level (ASL), cloud forest, date and leg unknown.

Comparative material: 1 male (21.8 × 13.2), ZRC 2015.0017, left G1. Complete structure, mesial view (Fig. 1C); distal part, mesiocephalic view (G). Ptychophallus tumimanus, male (21.8 × 13.2), ZRC 2015.0017, left G1. Complete structure, mesial view (D). Scales: 1 mm. me, mesial process; lp, lateral process.

Remarks: The G1 of the specimen examined closely resembles those studied by Magalhães et al. (2015), except that the mesial process is slightly bilobed on its distal border (Fig. 1A, C). The species also resembles Ptychophallus bilobatus sp. n., but the G1 morphology of the two species differs markedly in other characters (see Remarks of Ptychophallus bilobatus sp. n. for a detailed morphological comparison).

Ptychophallus tumimanus (Rathbun, 1898)

(Figs. 1D, 8)

Material examined: 1 male (21.8 × 13.2), ZRC 2015.0017, 1 male (23.5 × 14.5), INPA 2481 (from ZRC 2015.0018), Panama, Darién province, near Meteti, Reserva Hidrológica Filo del Tallo [~06°27ʹ06”N 78°58ʹ43”W], rainforest, ~163 m ASL, date and leg unknown.

Comparative material: 1 male, USNM 230099, Panama, Cocle province, El Valle, date unknown, P. Allen leg.

Distribution: Atlantic and Pacific drainages of central and southeastern Costa Rica and Pacific drainage of Panama. In Panama, the species is known from the western and central portions of Pacific drainage (Magalhães et al., 2015: 340, fig. 84); the present record extends its range towards the Darién province, eastern Panama (Fig. 8).

Remarks: The G1 of the specimen examined (Fig. 1D) is very similar to that described by Magalhães et al. (2015). In comparison with the specimen from El Valle (Coclé province) (USNM 230099) (Magalhães et al., 2015: 319, fig. 58), the G1 of the specimen has a lateral process with a slightly smaller and more rounded proximal lobe, but such difference is subtle and can be considered as intraspecific variability.

Ptychophallus bilobatus n. sp.

(Figs. 2, 3, 8)

Type material: Holotype: male (24.0 × 13.6), MZUSP 38799 (transferred from ZRC 2015.0022), Panama, Chiriquí province, Boquete, Bajo Mono [~08°48ʹ 46”N 82°27ʹ14”W], ~1,730 m ASL, cloud forest, date and leg unknown.


Figure 1. Ptychophallus colombianus, male (37.0 × 22.7 mm), ZRC 2015.0023, left G1. Complete structure, mesial view (A); distal part, lateral view (B); distal part, mesiocephalic view (G). Ptychophallus tumimanus, male (21.8 × 13.2), ZRC 2015.0017, left G1. Complete structure, mesial view (D). Scales: 1 mm. me, mesial process; lp, lateral process.
Diagnosis: G1 with distinct subdistal ridge; marginal process indistinct, continuous with mesiocaudal margin of apex, not produced beyond this margin. Mesial process bilobed, slightly downturned, proximal lobe larger, subtriangular, distal lobe smaller. Lateral process long, encompassing approximately 75% of stem length (measured from proximal opening to caudal border of apex), with distinct median concavity on caudal surface, moderately bilobed; proximal lobe rounded, as wide as distal lobe; distal lobe thicker distally, slightly wider than lateral end of apex, moderately swollen distally on cephalic surface.

Description of holotype: Carapace (Fig. 2A, B) outline ellipsoidal, widest medially (cw/cl 1.76), dorsal surface smooth, nearly flat, regions weakly defined. Two distinct gastric pits, close to each other, on metagastric region. Cervical grooves wide, deeper proximally, shallower distally, slightly arched, distal end not reaching anterolateral margin. Postfrontal lobules small, nearly indistinct; median groove barely visible. Surface of carapace between front, postfrontal lobules smooth, distinctly deflected anteroven- trally. Upper border of front (Fig. 2C) indistinct, median notch
absent (larger male paratype with upper border of front distinct, rounded, smooth, nearly straight in dorsal view); lower border carinate, slightly sinuous in dorsal view, nearly straight in frontal view. Upper orbital margin smooth towards inner side, lined with faint papillae towards outer side; lower orbital margin crenulate, lined with faint papillae; exorbital angle low, obtuse. Anterolateral margin of carapace with small notch just posterior to exorbital angle, followed by set of vestigial, rounded teeth decreasing in size from anterior to posterior portion; pterygostomial region densely pilose (Fig 2C). Suborbital, subhepatic regions of carapace sidewall smooth; pterygostomial regions densely pilose (Fig 2B, C).

Endopod of mxp3 (Fig 2D) with ischium trapezoidal, inner margin nearly straight, outer margin slightly convex; merus subrectangular, outer margin with distolateral corner broadly rounded, inner surface of 3-articulated palp having setae; exopod of mxp3 long, narrow, 0.73 times length of outer margin of ischium. Inner surface of 3-articulated palp having setae; exopod of mxp3 rectangular, outer margin with distolateral corner broadly rounded, fused to caudal surface, forming distinct subdistal caudal ridge; straight in mesial view, with scattered bristles; apex bent approximately 18 °

abdominal sternites of mxp3, first pereiopods (sternites III, IV, V) completely fused, except for small notches at lateral edges of sternites; s4/s5, s5/s6 not reaching midline of thoracic sternum by magalhães et al. (2015) with regards to some characters of the G1. In both species, the lateral process is quite long (approximately 70–80%) comparatively to the length of the whole stem, with the proximal and distal lobes separated by a shallow concavity. The bilobed mesial process is also a character shared by these two species. Although all specimens attributed to P. colombianus by magalhães et al. (2015) have a G1 with unilobed mesial process, the G1 of the specimen examined possesses a slightly bilobed mesial process (Fig 1A, C). Petychothallus bilobatus sp. n. and P. colombianus can nevertheless be distinguished from each other by the following important G1 characters: 1) distal lobe of the lateral process is wider than the lateral end of the apex and is distinctly swollen distally, as well as slightly overlapping the cephalic margin of apex in P. bilobatus sp. n. (Fig 3A, B) (only slightly narrower than the lateral end of the apex, moderately swollen distally and clearly shorter than the cephalic margin of apex in P. colombianus; Fig 1A); 2) apical notch at the mesiocaudal margin of the apex in P. bilobatus sp. n. (Fig 3A) (at the lateral end of the apex in P. colombianus; Fig 1A); 3) distal portion of the marginal suture is directed to the caudal side in P. bilobatus sp. n. (Fig 3A) (directed to the cephalic side in P. colombianus; Fig 1A); and 4) marginal process is indistinct and continuous with the mesiocaudal margin of apex in P. bilobatus sp. n. (Fig 1A) (short, rounded, slightly discontinuous from mesiocaudal margin of apex in P. colombianus; Fig 1A).

A bilobed mesial process is also present in the G1 of P. costaricen sis villalobos, 1974, a species so far known only in central-southern Costa Rica (Magalhães et al., 2015), but its G1 differs from that of P. bilobatus sp. n. mainly by 1) the proximal and distal lobes of the lateral process are clearly divided by a deep median cleft and are subequal in length and width in P. costaricensis (cf. Magalhães et al., 2015: figs. 15, 16), whereas in P. bilobatus sp. n., the lobes are only separated by a shallow concavity and the distal lobe is
larger than the proximal one (Fig. 3A, B); 2) marginal process is more developed and slightly discontinuous with the caudal margin of the apex, reaching a little beyond this margin in P. costaricensis (cf. Magalhães et al., 2015: fig 16), whereas it is indistinct and continuous of the caudal margin of the apex in P. bilobatus n. sp. (Fig. 3A); and 3) presence of a short spine on the laterocephalic side of the mesial lobe (Magalhães et al., 2015: fig. 15), which is absent in P. bilobatus n. sp. (Fig. 3B).

The thick, swollen distal lobe of the lateral process that can exceed the cephalic border of the apex is also seen in the G1 of P. uncinatus Campos & Lemaire, 1999, but the lobes of the lateral process are clearly separated by a deep incision in this species, the mesial process is unlobed, and the distal portion of the marginal suture is directed to the cephalic side (Magalhães et al., 2015: figs. 61–63).

The distribution of P. bilobatus n. sp. in Chiriquí province, Panama and the overall resemblance of its G1 with the one attributed to P. colombianus might raise some doubts about the validity of the new taxon. Magalhães et al. (2015) considered that the validity of P. colombianus might be questionable because it was based on two female syntypes from the Chiriquí province (David River), and because there are at least two other species of Ptychophallus (P. paraxanthusi Bott, 1968 and P. montanus (Rathbun, 1890)) occurring in the same region of its type locality. Based on the morphological differences between the G1s of these three species, and to avoid nomenclatural instability, the authors recognized P. colombianus as a valid species. Similarly, the G1 of the specimens assigned to P. colombianus also show some differences in relation to that of P. bilobatus sp. n., as discussed above. On this basis, we have therefore decided that it is best to describe the present new species. We nevertheless note the suggestion by Magalhães et al. (2015) that a thorough molecular and morphological study of the species from the region with a larger series of specimens from a wider geographical coverage could be useful.


**Tribe Potamocarcinini** Ortmann, 1897

**Genus Potamocarcinus** H. Milne Edwards, 1853

Potamocarcinus tapirrhynchus n. sp.

(Figs. 4, 5, 8)

*Type material:* Holotype: male (36.5 × 24.2), MZUSP 38800 (from ZRC 2015.0019), Panama, Darién province, near Meteti, Reserva Hidrológica Filo del Tallo [~8°27’06”N 77°38’43”W], rainforest, ~163 m ASL, date and leg. unknown. Paratype: 1 immature male (20.5 × 14.2), ZRC 2015.0020, Panama, Darién province, near Meteti, Rio El Balsal, [~8°28’16”N 77°39’50”W], rainforest, ~110 m ASL, date and leg. unknown; 1 male (31.9 × 22.2), CoZEM-CR 66, Panama, Darién province, Rio Tüira, 08°01’08.11”N 77°44’06.83”W, 24 April 2014, leg. A. Cornejo, M. Molinar & A. Tuton.


*Diagnosis:* G1 straight in caudal, mesial views; marginal process shorter than mesial lobe on apical crest, situated at approximately same level of mesial process. Mesial process on distal portion of mesial border as stout, rounded projection overall obliquely directed apical-cephalically, only tip slightly curved downwards; mesial crest of apex produced into oblique, enlarged mesial lobe partially fused to mesial process in mesial view, slightly folded over apex cavity; cephalic surface with distal cephalic process as larger, conical tooth; proximal cephalic process as smaller, blunt tooth with few minute setae. Lateral process as subterminal low, blunt tooth. Distinct, short caudal ridge present on subterminal portion of caudal surface.

Figure 4. Potamocarcinus tapirrhynchus n. sp., holotype male (36.5 × 24.2 mm), MZUSP 38800. Habitus, ventral view (A); habitus, dorsal view (B); frontal view of cephalothorax (C); mxp3 (D); outer view of right chela (larger) (E). Scales: A, B = 10 mm; C–E = 5 mm. Photograph CM.
Description of holotype: Carapace (Fig. 4A, B) outline ellipsoid, widest medially (cw/cl 1.51), dorsal surface smooth, nearly flat, regions weakly defined. Two barely visible gastric pits, close to each other, on metagastric region. Cervical grooves shallow, wide, nearly straight, distal end barely reaching anterolateral margin. Postfrontal lobules small, nearly indistinct; median groove distinct, shallow. Surface of carapace between front, postfrontal lobules smooth, slightly deflected anteroventrally in dorsal, frontal views. Upper border of front carinate, slightly convex, lined with faint papillae, median notch V-shaped, deep; lower border carinate, lined with faint papillae, nearly straight in frontal view, not projected beyond upper one in dorsal view. Upper, lower orbital margins carinate, lined with faint papillae; exorbital angle low, obtuse. Anterolateral margin of carapace with conspicuously shallow notch at level of distal portion of cervical groove, followed by row of minute, rounded teeth increasing in size from anterior to posterior portion; posterolateral margin smooth, marked by faint suture. Epistome narrow; epistomial tooth low, strongly deflected lateroventrally, with carinate, smooth borders, tip rounded (Fig. 4C). Suborbital, subhepatic regions of carapace with few scattered small setae, otherwise smooth; pterygostomial regions densely pilose (Fig. 4A).

Endopod of mxp3 with ischium subquadrate, inner margins straight, outer margin slightly convex; merus subtrigonal, outer margin with distolateral corner rounded, inner surface of 3-articulated palp with setae; exopod of mxp3 moderately long, narrow, 0.52 times length of outer margin of ischium (Fig. 4D). Aperture of efferent branchial channel wide, subcircular, outer margin somewhat sinuous, smooth (Fig. 4C, D).

Chelipeds (Fig. 4A, B) moderately heterochelous, similarly armed, right P1 largest. Larger cheliped with merus subtriangular in cross section; upper margin rounded, with irregular row of low, squamous teeth, slightly larger distally; inner lower margin lined by longitudinal row of conical tubercles increasing in size distally; outer lower margin with single row of small tubercles; distal upper margin arched, smooth, lower margin with subdistal row of small tubercles. Carpus with inner margin with prominent median spine, row of faint tubercles proximally, distally; outer surface rounded, smooth. Palm (Fig. 4E) slightly swollen (length/width 1.79); inner, outer surfaces, lower margin irregular mostly smooth, only few faint tubercles proximally. Fingers of both chelae (Fig. 4B) not noticeable gaping; tips slightly crossing on smaller chela; larger chela with large, subtriangular tooth proximally, followed by set of smaller, rounded ones. Dactylus of larger chela moderately arched, slightly shorter than polex, slightly longer than palm (dactylus/palm 1.3, measured dorsally); surfaces of dactylus, polex smooth, except for scattered punctuations with minute setae (Fig. 4E). P2–5 slender, ratios dactylus/propodus, dactylus/merus (left side measurements), respectively, as follows: P2 = 1.58, 0.85; P3 = 1.56, 0.79; P4 = 1.61, 0.85; P5 = 1.76, 0.94. P2–5
with dactyls having 5 longitudinal rows of sharp, corneous spines, increasing in size distally, 2 faint grooves on proximal external surface.

Thoracic sternum nearly as long as broad (Fig. 4A). Thoracic sternites of mxp3, first pereiopods (sternites III, IV) completely fused, except for small notches at lateral edges of sternum; s4/s5, s5/s6, s6/s7 as shallow groove laterally; medially, deeper at level of reaching midline of thoracic sternum; s7/s8 complete, marked by shallow groove reaching midline of thoracic sternum. Midline of thoracic sternum flat, wide at somites V–VI, as deep groove between somites VII, VII, deeper at somite VII. Episternites 4–7 subtriangular posteriorly. Male sternopleonal cavity subtriangular, densely pilose in region around pleononal holding system. Tubercle of pleonal holding system small, placed near border of sternopleonal cavity, adjacent to s5/s6. Penis somewhat long, slender, hook-shaped distally, emerging from nearby coxo-ster nal condyle articulation, located proximally on sternite 8.

All pleonal somites free; lateral margins of somites fringed by row of short setae; male pleon with somite VI trapezoidal, longest, slightly longer than telson (ratio length somite VI / length telson = 1.1), lateral margins slightly concave (Fig. 4A). Male telson subtriangular, as long as wide, approximately as long as pleonal somite VI, lateral margins slightly concave medially, fringed by row of short setae become sparser distally; tip rounded (Fig. 4A).

G1 (Fig. 3) straight in caudal, mesial views, moderately compressed mesio-latero-sagittally, slightly narrower approximately medially. Mesial border nearly straight in mesial view; mesio-cephalic surface with dense subdistal longitudinal patch of short setae increasing size distally. Marginal plate medially fused to caudal surface, delimited by incomplete lateral suture marked by distinct sulcus on proximal half of stem, with few short, long setae. Marginal suture on mesial side, slightly sinuous, with dense row of short, long marginal setae proximally; marginal process broad, roughly subrectangular, shorter than mesial lobe of apical border, situated at approximately same level of mesial process. Mesial process on distal portion of mesial border as stout, subtriangular projection overall obliquely directed apical-cephalically, only with rounded tip slightly curved downwards. Apex moderately compressed in mesio-lateral direction; apical crests asymmetrical in height along median portion of apex, mesial crest slightly more produced distally than lateral one; mesial crest produced into oblique, enlarged mesial lobe towards cephalic side being slightly folded over apex cavity, partially fused to mesial process in mesial view; lateral crest produced into small, rounded distostephalic lobe; mesial lobe, distostephalic lobes ending symmetrically on cephalic side, separated by small depression. Spermathecal channel opening situated apically, positioned closer to caudal end. Field of apical spines weakly developed, with small patch of few minute spines mostly around spermathecal channel. Cephalic surface with distal cephalic process as larger, conical tooth with rounded tip; proximal cephalic process as smaller, blunt tooth with few minute setae. Lateral process as subterminal low, blunt tooth. Distinct, short caudal ridge present on subterminal portion of caudal surface.

Left G2 slightly shorter than G1, flagellum conspicuously slender, regularly tapering.

**Etymology**: The specific epithet is composed of tapir, the vernacular name of a South American mammal Tapirus terrestris (Linnaeus, 1758), which has a peculiar, large, curved snout, and rhynchos, Greek for snout or muzzle, in reference to the shape of the mesial process of the G1 that resembles a tapir’s muzzle in mesial view (Fig. 5A). The name is used as a noun in apposition.

**Type locality and distribution**: Panama, Darién province, near Meteti, Reserva Hidrológica Filo del Tallo, rainforest, ~163 m ASL (Fig. 8).

**Remarks**: The new species is assigned to Potamocarcinus H. Milne Edwards, 1853 on account of exopod of mxp3 being approximately half the length of the outer margin of the ischium; the mesial lobe of the G1 on the distal crest of the mesial surface extends beyond the apex; the G1 has a cephalically directed, well-developed mesial process; the cephalic process is composed of subdistal spines; and the field of apical spines is terminally located, positioned below or partially along the distal crests of the mesial and lateral surfaces (Magalhães et al., 2015).

Potamocarcinus tapirrhynchus n. sp. can be readily distinguished from congeners by the upwardly directed mesial process of the G1, which is partially fused to the mesial lobe of the apical crest (Fig. 5A). Although the distal end is slightly recurved downwards, the overall position of the mesial process as a whole is obliquely directed upwards and towards the cephalic side relative to the main axis of the stem. Except for *P. nicaraguensis* Rathbun, 1893 and all other congeners, this process is positioned transversally (Pretzmann, 1975: pl. 6; Alvarez & Villalobos, 1998: fig. 4a, b; Campos & Lemaître, 2002: fig. 2; Rodríguez & López, 2003: fig. 2; Campos, 2005: figs. 99, 100; Magalhães et al., 2015: figs. 71–76) with regards to the stem axis. The mesial process of the new species is also slightly upwardly directed like in *P. nicaraguensis*, thus having a rounded distal end. Both species, however, can be easily distinguished because the mesial process is totally fused to the weakly developed mesial lobe in *P. nicaraguensis*, making their borders fully continuous (Magalhães et al., 2015: figs. 73, 74), whereas the mesial process is only partially fused to the mesial lobe in *P. tapirrhynchus* n. sp., making their borders slightly discontinuous (Fig. 5A). Their G1s also differ by the form of the marginal process, which is subtriangular and distinctly longer than the mesial lobe in *P. nicaraguensis* (Magalhães et al., 2015: fig. 73), and subrectangular and shorter than mesial lobe in *P. tapirrhynchus* n. sp. (Fig. 5A).

In addition to the generic diagnostic characters, *P. tapirrhynchus* n. sp. resembles the other two species of the genus known to occur in Panama, *P. richmondii* (Rathbun, 1893) (Magalhães et al., 2015: fig. 75) and *P. lobulatus* Campos & Lemaître, 2002 (Campos & Lemaître, 2002: fig. 2A) in having a G1 with a subrectangular marginal process, shorter than the mesial lobe and not produced apically beyond the apical cavity, and with a longitudinal patch of short setae along the subdistal portion of the meso-cephalic surface (Fig. 5A, B). These species can be distinguished from each other mainly by characters of the mesial process, mesial lobe, and lateral process of the G1 (Table 1).

Judging from the published illustrations of *P. colombiensis* Práhl & Ramos, 1987 (Práhl & Ramos, 1987: fig. 1) and *P. pinzonii* Campos, 2003 (Campos, 2003: figs. 1A), the G1s of the two Colombian species of Potamocarcinus resemble that of the new species by having a marginal process that is shorter than the mesial lobe, and the cephalic surface with distal and proximal cephalic processes. *Potamocarcinus tapirrhynchus* n. sp. cannot nevertheless be distinguished from these species by the overall direction of the mesial process, the rounded distal end of the mesial process, and the lower mesial lobe.

**Nomenclatural statement**: A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:8B41D3D2-7EA5-433D-8D69-7D513A759ED2.

**Emberacarcinus n. gen.**

**Diagnosis**: Exopod of mxp3 approximately 0.5 times length outer margin of endopodal ischium. Orifice of exopodal branchial channel open, with pyriform outline. G1 with lateral margin concave, with distinct rounded protuberance proximally, irregular row of minute spines along distal half; apex broadened by rounded protuberance with minute spines on caudalateral surface; apex cavity narrow, elongated caudocephalically, partially covered by folding of mesial lobe mesial lobe short, oblique to main axis of apex, folded in laterocephalic direction; mesial process triangular,
prominent, recurved cephalically, tip directed downwards; cephalic surface with small, conical cephalic process between mesial, lateral processes; lateral surface with large, prominent, subtriangular lateral process with minute spines scattered along rounded margins.

**Type species**: *Potamocarcinus darienensis* Magalhães, Campos & Türkay, 2013, by present designation and monotypy.

**Species included**: *Emberacarcinus darienensis* (Magalhães, Campos & Türkay, 2013) n. comb.

**Distribution**: Eastern Panama, Darién province (Fig. 8).

**Gender**: Masculine.

**Etymology**: The generic name is formed by the combination of Emberá, the Panamanian indigenous people, Emberá-Wounaan, who live in the Darién province, the region inhabited by the type species of the genus, and carcinus, from the Greek karkinus, in reference to the giant crab that, according to Greek mythology, helped Hydra in the battle against Herakles at the lake of Lerna.

**Material examined**: Male (20.5 × 12.7), paratype of *Emberacarcinus darienensis* n. comb., INPA 1983, Panama, Darién province, Cerro Mali, Serranía de Darién, 1400 m, 18.1.1975, C.W. Myers.

**Remarks**: The morphology of the G1 of *E. darienensis* n. comb. shows some peculiarities that do not agree very well with the morphology of a typical *Potamocarcinus*-type G1. These differences became clear during our study to assess the affinities of the G1 of *Potamocarcinus darienensis*. Several morphological features characterize the G1 of *Emberacarcinus* n. gen. (see Magalhães et al., 2013: fig. 1C-F), which distinguishes it from the G1 of *Potamocarcinus* as follows: 1) the lateral border bears a distinct rounded protuberance proximally (proximal portion of the lateral border is continuous and this protuberance is absent in *Potamocarcinus*); 2) the apex is narrow mesiolaterally and broadened on the caudal lateral surface by a rounded protuberance with minute spines (apex is usually elongated mesiolaterally in *Potamocarcinus*, with its caudal lateral surface narrower than in *Emberacarcinus* n. gen.); 3) the mesial lobe on the distal crest of the mesial surface is shorter than the marginal process in mesial view (mesial lobe is usually distinctly longer than the marginal process, except in *P. nicangensis*, in *Potamocarcinus*); 4) the mesial process is directed downwards regarding the main axis of the stem (transverse or slightly directed upwards relative to the main axis of the stem in *Potamocarcinus*); and most importantly, 5) a large, strong, subtriangular lateral process (proximal process

**Table 1.** Main morphological differences among the male first gonopod (G1) of the Panamanian species of *Potamocarcinus*.

<table>
<thead>
<tr>
<th></th>
<th><em>P. tapirhynchos</em> sp. n.</th>
<th><em>P. richmondi</em> (Rathbun, 1893)</th>
<th><em>P. lobulatus</em> Campos &amp; Lemaître, 2002</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mesial process:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Direction relative to main axis</td>
<td>Obliquely directed upwards</td>
<td>Tranversal</td>
<td>Tranversal</td>
</tr>
<tr>
<td>Shape of distal end</td>
<td>Rounded</td>
<td>Acute</td>
<td>Acute</td>
</tr>
<tr>
<td><strong>Mesial lobe:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Position along mesial crest of apex</td>
<td>Displaced to cephalic side</td>
<td>Displaced to caudal side</td>
<td>Median</td>
</tr>
<tr>
<td>Position relative to marginal process</td>
<td>Slightly higher</td>
<td>Distinctly higher</td>
<td>Distinctly higher</td>
</tr>
<tr>
<td>Shape</td>
<td>Wide, mostly straight, rounded near cephalic end</td>
<td>Narrow, subquadrate</td>
<td>Wide, rounded</td>
</tr>
<tr>
<td>Lateral process</td>
<td>Low, blunt tooth</td>
<td>Indistinct</td>
<td>Low, blunt tooth</td>
</tr>
</tbody>
</table>

**Distribution**: Eastern Panama, Darién province (Fig. 8).

**Gender**: Masculine.

**Etymology**: The generic name is formed by the combination of Emberá, the Panamanian indigenous people, Emberá-Wounaan, who live in the Darién province, the region inhabited by the type species of the genus, and carcinus, from the Greek karkinus, in reference to the giant crab that, according to Greek mythology, helped Hydra in the battle against Herakles at the lake of Lerna.

**Material examined**: Male (20.5 × 12.7), paratype of *Emberacarcinus darienensis* n. comb., INPA 1983, Panama, Darién province, Cerro Mali, Serranía de Darién, 1400 m, 18.1.1975, C.W. Myers.

**Remarks**: The morphology of the G1 of *E. darienensis* n. comb. shows some peculiarities that do not agree very well with the morphology of a typical *Potamocarcinus*-type G1. These differences became clear during our study to assess the affinities of the G1 of *Potamocarcinus darienensis*. Several morphological features characterize the G1 of *Emberacarcinus* n. gen. (see Magalhães et al., 2013: fig. 1C-F), which distinguishes it from the G1 of *Potamocarcinus* with minute spines scattered along its rounded margins (lateral process is reduced to a small, blunt tooth, sometimes vestigial or even absent in *Potamocarcinus* (see Pretzmann, 1972, 1975; Rodriguez, 1982; 2001; Prahl & Ramos, 1987; Campos & Lemaître, 2002; Alvarenga & Villalobos, 1998; Campos, 2003; Rodriguez & López, 2003; Magalhães et al., 2015). The diagnosis of *E. darienensis* n. comb. offered by Magalhães et al. (2013) reflects these generic differences and can be used to distinguish the species from *P. tapirhynchos*.


**Trichodactylidae** Latreille, 1828

**Subfamily Trichodactylinae** H. Milne Edwards, 1853

**Trichodactylus quinqueidentatus** Rathbun, 1893 (Figs. 6, 7, 9)

**Material examined**: 1 male (21.6 × 17.9), USNM 285033, Honduras, Gracias a Dios department, Rio Patuca (~15°41’N 84°22’W), near the town of Brus Laguna, 05.viii.1975, leg. R.R. Miller, F.H. Miller, R.K. Johnson, G.K. Gloder, D.W. & T. Greenfield; 1 male (21.2 × 18.9), ZRC 2015.0021, Panama, Darién province, near Meteti, Quebrada El Loro (~08°28’26”N 77°59’23”W), rainforest, ~30 m ASL, date and leg unknown.

**Comparative material**: 2 males (15.8 × 12.7; 19.8 × 17.2), 2 females (16.9 × 14.6; 21.5 × 18.2), INPA 311, Colombia, Magdalena Department, Sevilla River (~10°52’02”N 74°18’04”W), tributary of the Ciénaga Grande de Santa Marta, 24.x.1978, leg. M. Türkay.

**Description**: Carapace (Fig 6A, B) subcircular, smooth, convex longitudinally; lateral margin with 5 low, sharp teeth decreasing in size posteriorly. Orbit with lower margin smooth, interrupted by distinct sinus about ¼ distance from lateral angle of orbit, with sharp, medially curved tooth (Fig 6C, D). Pleural somites free, lateral margins slightly concave. Telson (Fig 6B) subtriangular, lateral margins discontinuous with those of pleonal somite VI. G1 (Fig 7) straight, with median constriction; proximal portion wider than distal portion; distal portion tubular, with dorsal, ventral margins subparallel, slightly convex in mesial view, with field of subterminal spines divided into caudal, cephalic patches. Marginal suture straight, situated along mesial surface. Apex nearly symmetrical, distal margin nearly straight; distal opening subtriangular, wide, directed mesially; few apical setae situated subdistally on dorsal side, distally on lateral side, as well as in inner side of distal opening.
The species has a disjunct distribution in Central (Honduras, Nicaragua, and Panama) and South America (central, north-northwestern Colombia) (Smalley & Rodríguez, 1972; Rodríguez, 1992; herein) (Fig. 9). It was described on the basis of a single female from Bluefield, on the Atlantic coast of Nicaragua (Rathbun, 1893), and subsequently found in several localities in the Magdalena, Sinú, and Meta rivers basins in Colombia (Campos, 1985, 2005, 2009, 2010, 2014; Smalley & Rodríguez, 1972). These first records of *T. quinquedentatus* in Honduras and Panama could indicate that its distribution could be nearly continuous throughout the whole range, and its absence in some areas might be the consequence of poor collecting efforts. It should be noted, however, that the species has not yet been found in well-explored regions of central and western Panama (Abele & Kim, 1989; Ábrego & Cornejo, 2015), as well as in Costa Rica, where recent intensive surveys of the freshwater crab fauna yielded no trichodactylids (Magalhães et al., 2010, 2015; Lara et al., 2013). As such, the disjunct distribution of this species may well be real. It is also intriguing that no additional specimens of *T. quinquedentatus* have been found in Central America in nearly a century following its description by Rathbun (1893), although it inhabits lowland areas of relatively easy access.

The disjunct, transbasin distribution of *T. quinquedentatus* in Honduras, Nicaragua, Panama, and Colombia raises some taxonomic, evolutionary, and biogeographical issues. Do the populations from Honduras to central Colombia belong to the same species? Is the genetic distance between these populations greater than what could be considered interspecific variability? Regardless of whether these populations represent one or more than one closely related taxon, how did these populations reach their current distribution, which vicariant event (or events) could have caused this divergence and posterior dispersion, where has this lineage originated and evolved, what was its dispersal route (from South America to Central America or vice versa, and which would be their closest phylogenetic affinities, South American or Mesoamerican Trichodactylinae? These are questions that may impact our understanding of the complex geological, ecological, and biogeographical history of Central America and northwestern South America (see Hoorn et al., 1995, 2010; Lundberg et al., 1998; Iturralde-Vinent & MacPhee, 1999; Albert et al., 2006; Kirby et al., 2008; Hoorn & Wesselingh, 2010; Albert & Reis, 2011; Farris et al., 2011; Montes et al., 2012, 2015; Leigh et al., 2014; Bacon et al., 2015; Hoorn & Flantua, 2015; Rodríguez Tribaldos et al., 2017).
Figure 8. Occurrence of *Emberacarcinus darienensis* Magalhães, Campos & Türkay, 2013, n. comb. (cross), *Ptychophallus bilobatus* n. sp. (red diamond), *P. colombianus* (circle), *P. taminanus* (square), and *Potamocarcinus tapirrhynchus* n. sp. (star) in Panama (previous records according to Magalhães et al., 2013, 2015). This figure is available in color at *Journal of Crustacean Biology* online.

Figure 9. Distribution of *Trichodactylus quinquedentatus* (red star: type locality; red square: new records; black circle: previous records according to Smalley & Rodriguez, 1972; Campos, 1985, 2005, 2009, 2010, 2014). This figure is available in color at *Journal of Crustacean Biology* online.
The current transbasin distribution of *T. quinquedentatus* in Colombia (Campos, 2014) suggests that it should have been present in the proto-Orinoco-Amazonas system, a large northwesterly directed fluvo-lacustrine system flowing towards the Caribbean and extending south to north along the foreland basins of the emerging Central Andes, a landscape that dominated much of northern South America, with the northwestern lowlands alternating between freshwater environments and brackish marine embayments due to episodic marine transgressions, from the middle Eocene to Oligocene (43–24 mya) [see Hoorn et al., 1995, 2010; Lundsberg et al., 1998; Albert et al., 2006; Wesselingh et al., 2010; Albert & Reis, 2011; Wesselingh & Hoorn, 2011; Rodriguez Trilhals et al., 2017, and references therein for details on the paleogeomorphology and landscape evolution of South America]. When the present-day Rio Magdalena basin was isolated from this system by the uplift of the Eastern Andean Cordillera during the early-middle Miocene (24–11 mya), the distribution of *T. quinquedentatus* was split into two areas: central Colombia, restricted to the upper tributaries of Rio Meta (Rio Orinoco basin), and a larger area in the Magdalena and Sinú river basins in north-northwestern Colombia (Campos, 2005, 2014) (Fig. 9). The origin of the species could thus be extended back at least to the Oligocene (34–24 mya). Assuming that the species was distributed in southwestern South America at that period, it could have reached eastern Panama and Mesoamerica after the complete closure of the Central American Seaway in the middle Miocene (24–15 mya) (Hoorn & Flantua, 2015; Montes et al., 2015). Such event, however, could have taken place even earlier. Molecular biology studies involving several taxa indicate that cross-Isthmian migrations occurred in incremental pulses over an extended period and were probably correlated with the gradual formation and emergence of the Isthmus of Panama (Bacon et al., 2015). Although their study did not include crustaceans, the rates of dispersal estimated by Bacon et al. (2015) for groups with similar limited dispersal abilities, such as freshwater fishes and amphibians, showed a cross-Isthmian migration occurring since the early-middle Eocene, with two statistically significant migration rate shifts at around 6.5 and 24 mya. The length of time involved, however, has not resulted in any obvious morphological differences between the two populations.

Answers to these questions and a consistent hypothesis to explain the historical biogeography of the Mesoamerican trichodyactylidsh should only be available after comprehensive molecular and morphological studies based on a more abundant series of specimens from the complete distributional range of the species.

ACKNOWLEDGEMENTS

CM expresses his gratitude to Aydén Cornejo and Edgar Pérez (CoZEM) and Rafael Lemaire and Karen Reed (USNM) for their assistance during visits to their respective institutions, and to José Luis Villalobos (Universidad Nacional Autónoma de México) for his comments on the new genus. The late Gilberto Rodríguez facilitated the access of CM to an unfinished manuscript by the late Alfred E. Smalley from which the illustration of the G1 of *Trichodactylus quinquedentatus* from Honduras (USNM 285055) was reproduced. CM also thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) for an ongoing research grant (304736/2015-5). Thanks are due to Mohammad Dzaki and José Christopher Mendoza (ZRC) and Marcos Tavares (MZUSP) for curatorial support. We acknowledge the valuable comments by the anonymous reviewers and the editors, which greatly improved the manuscript.

REFERENCES


FRESHWATER CRABS FROM CENTRAL AMERICA


